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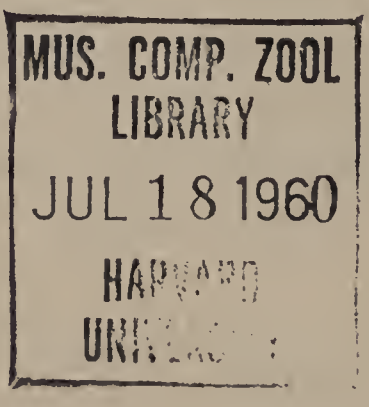

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CORRIGENDUM

Page 151 "Key to females" § 2 lines 1, 2 and 4 and
Page 152, lines 15, 17 and 20: For "hind femur" read "hind tibia".

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TRANSACTIONS OF THE SOCIETY
FOR BRITISH ENTOMOLOGY

VOL. 13 | 11TH FEBRUARY, 1958 | PART 1

THE LIFE HISTORY AND BEHAVIOUR OF *COLEOPHORA ALTICOLELLA* ZELL. (LEP.)

By A. M. JORDAN, Ph.D.

(Department of Zoology, Durham Colleges in the University of Durham*)

1. Introduction

During 1952-4 a study of the relationship between the moor-rush *Juncus squarrosus* L., and the Lepidopteron, *Coleophora alticolella* Zell. whose larvae feed on the seeds of this plant, was carried out on the Moor House Nature Reserve in Westmorland (Nat. grid. ref. 35/375532). This paper records results obtained concerning various aspects of the life history and behaviour of *C. alticolella.*

J. squarrosus is a common component of the flora of the area and occurs even on the highest ground in the vicinity (Cross Fell, 2,930 ft. O.D.). The lower limit of the rush appeared to be largely determined by the upper limit of cultivation; in this area about 700 ft. on the western slope of the Pennines, and about 1,500 ft. on the eastern slope. The moth larvae were abundant in the rush capsules but, during the years of the investigation, were never recorded about 2,170 ft. and above 1,800 ft. larvae were sparse.

Works by Stainton (1859), Wood (1892), Sich (1921/2/3), Waters (1928) and Hackman (1941 and 1948) each give some information on *C. alticolella.* Bradley (1955) showed that the name *Coleophora caespititiella* Zell. had been wrongly applied to the species commonly associated with *J. squarrosus.* His study of the genitalia of Zeller's type material indicated that this species is *C. alticolella* Zell., and the genitalia of specimens taken in the course of the present work agree with Bradley's description of *C. alticolella.*

2. Life History

(a) *Ovum*

In 1953 adult *C. alticolella* first appeared on 3rd June and the first eggs were observed on the rush stems on 5th June. The corresponding dates in 1954 were 8th June (although one was collected on 31st May) and 9th June.

The eggs were laid when the flowers of *J. squarrosus* were fully formed, although in many areas not yet opened. (At this stage the flowering stems had not attained their full height; for instance at 1,100 ft., at the time of the

* Present address: The West African Institute for Trypanosomiasis Research, Kaduna, N. Nigeria.

beginning of oviposition in the summer of 1953, the stems were four to six inches in height, less than half as tall as they became when fully grown.) Wood (1891) described the act of oviposition in the following terms: "the parent moth insinuates her thin, pointed ovipositor within the perianth of a floret, and affixes an egg to the inner surface of a segment." The present observations showed that eggs were also laid in the angle between two adjacent flowers. Presumably the position where the eggs were laid partly depended on the developmental stage of the flower at the time—if not sufficiently open it was probably impossible for the ovipositor to pass between two perianth segments of a flower. It was observed that eggs laid at the upper limit of the insect's range, where flowering of the rush was somewhat later than at lower altitudes, were generally found between adjacent flowers rather than within any one flower.

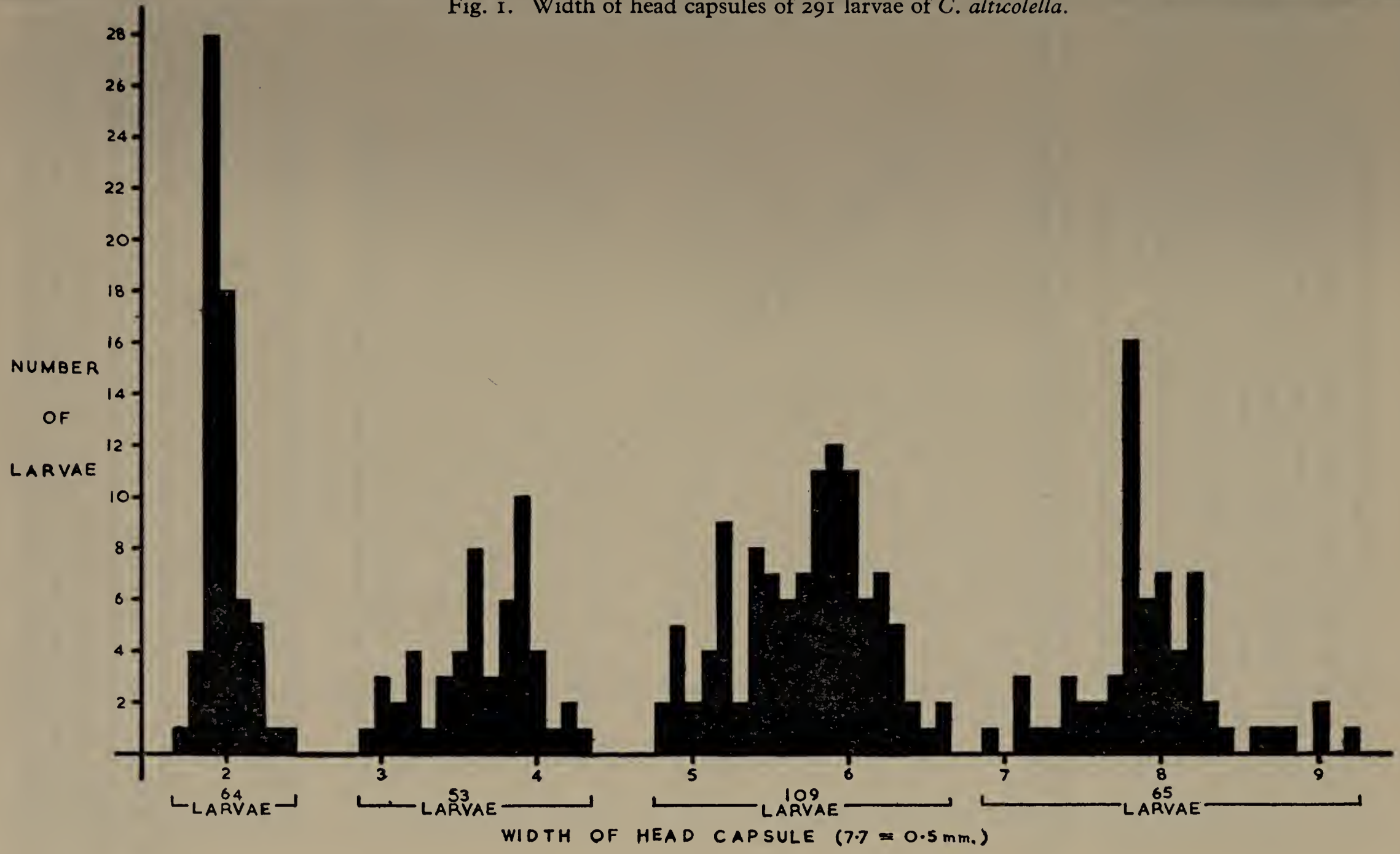
Sich (1922) suggested that the egg stage in Coleophoridae lasted 10 to twenty-one days. In 1953 the first eggs were found on 5th June whereas the first larva, and then only one individual amongst about fifty eggs, was not recorded until 30th June. In 1954 the corresponding dates were 9th June and 17th July. It is suggested that the later hatching in 1954 was caused by the cool weather prevailing during that period. That temperature had an important effect on the duration of the egg stage was shown by an experiment in which eggs kept at room temperature hatched a week after they were deposited, practically a month in advance of eggs in the field.

Adult moths were observed ovipositing practically up to the date of their disappearance for the season and viable eggs were found on the rush heads, in 1953, after mid-July, and in 1954 some were still present in mid-August. There was, therefore, a considerable time between the hatching of the first and last eggs in each area.

(b) *Larva*

Larvae of *C. alticolella* usually feed on the seeds of *Juncus squarrosus* L. and *J. effusus* L., but have also been recorded from *J. conglomeratus* L. (Stainton, 1859, Wood, 1892), *J. inflexus* L. (Stainton, 1859, Waters, 1928), *J. articulatus* L. (Waters, 1928), *J. compressus* Jacq. (Wood, 1892), and *Luzula pilosa* (L.) Willd. (Stainton, 1859) (the nomenclature of the original references has been modified to conform with that of Clapham, Tutin and Warburg, 1952). In the study area the most commonly utilised food-plant was *J. squarrosus*, but larvae were also observed on *J. effusus*, *J. articulatus* and *Luzula campestris* (L.) Br. *J. effusus* was widespread over the area, but was a less important food-plant than *J. squarrosus*. *J. articulatus* occurred on those areas of the Nature Reserve below about 1,100 ft. on the western Pennine slopes, but only very small numbers of larvae were observed feeding on this rush. No previous record of *C. alticolella* feeding on *L. campestris* has been found, but the number of larvae observed on this food-plant was low compared to the abundant larvae on nearby *J. squarrosus*. It is suggested that the larvae found on *J. articulatus* and *L. campestris* were individuals which had migrated from neighbouring *J. squarrosus* stems (see page 11). No oviposition was observed on either species and no eggs were found on the numerous stems examined.

Fig. 1. Width of head capsules of 291 larvae of *C. alticolella*.



The term "rush" in the following account refers to *J. squarrosus*.

On hatching, the first instar larvae bored into the rush capsules which by this time, and especially at the lower levels, had mostly attained their maximum size. The contained seeds were green and soft and easily penetrable by first-instar larvae. The first six weeks or so of larval life were spent within the confines of one rush capsule. The precise time spent feeding within the original capsule was partly dependent on the condition of this capsule; ripening seeds were a good food-source, but seeds degenerating, possibly through lack of fertilisation, were not. In the latter capsules very small early-instar larvae were found very late in the season.

Normally only one larva was found within a rush capsule, but in certain areas where larval infestation was heavy up to four larvae per capsule occurred.

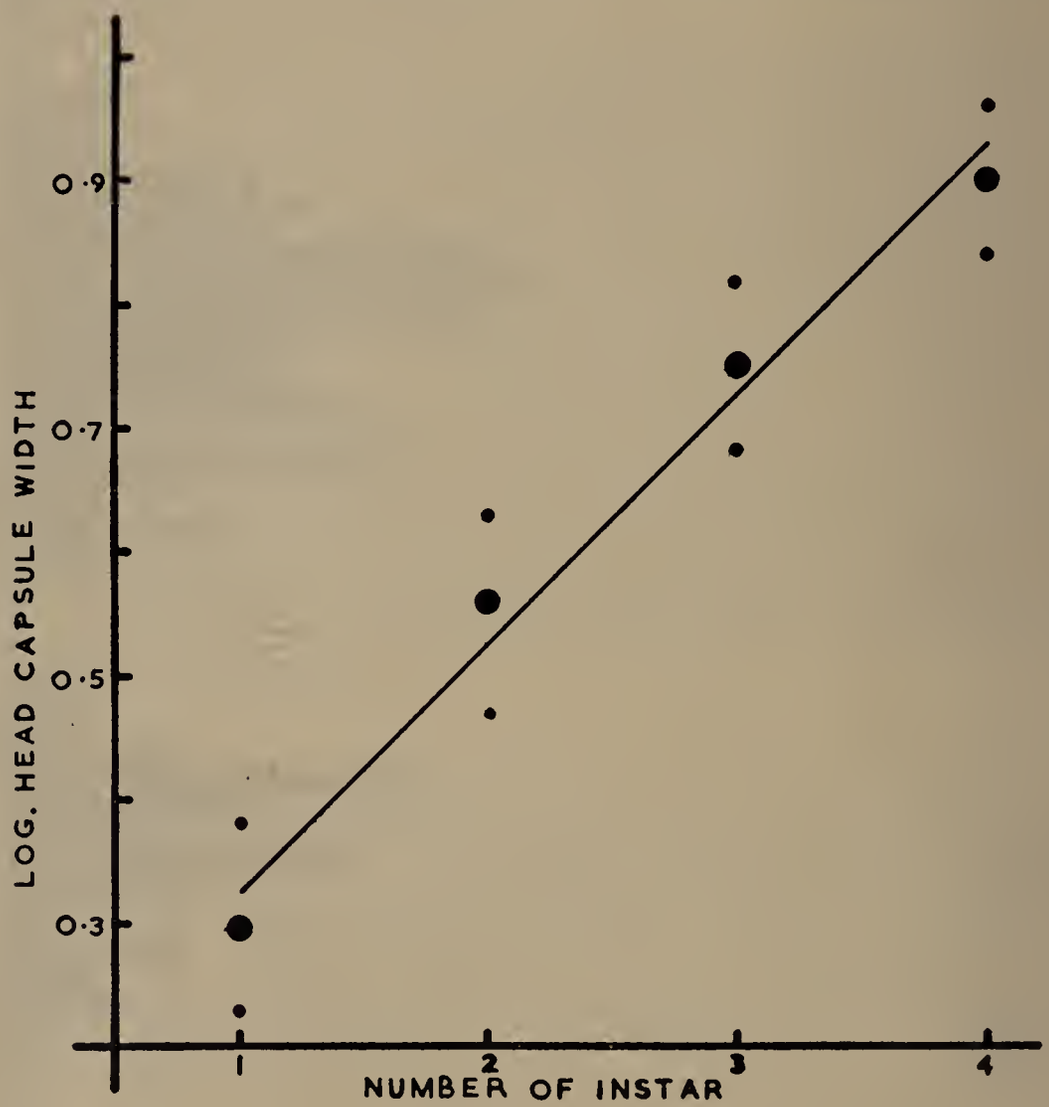


Fig. 2. Logarithm of mean head capsule width of the 4 postulated instars of *C. alticolella*. The observed extreme values for each instar are also shown.

Sich (1923) suggested that the Coleophoridae generally have five larval instars. This has been shown not to be the case, at least in *C. alticolella*. Measurements of the head-capsule widths of 291 larvae obtained from the field were made by mounting the heads in lactic acid, and examining them under a microscope with a graduated eyepiece. The existence of four clearly defined size-groups was shown (fig. 1). The arithmetic averages (utilising the arbitrary eyepiece units of fig. 1) of each of the four sets of figures has been taken and plotted, on a logarithmic scale, against the number of instars

(fig. 2). Dyar's Law (Dyar, 1890) assumes there to be a constant progression factor by which each instar increases in size over the preceding instar. In the present case, as is shown by the failure of the points to conform to the theoretical straight line included on fig. 2, there is a slight decrease in the factor between succeeding instars. Following the more recent practice (see, for example, Forbes, 1934) of expressing progression factors as the inverse of the original formulation by Dyar, by dividing the head-capsule width before moulting into the width after moulting, the progression factors between the four postulated instars of *C. alticolella* have been calculated. They are 1·84, 1·57 and 1·39.

There is considerable evidence from previous workers on Lepidoptera, amongst them Ripley (1923), Forbes (1934) and Beck (1950), and also Calvert (1929) on Odonata, that "the suppose constant factor is not actually constant but tends to decline in succeeding instars" (Beck, 1950). Beck pointed out that the data used by Dyar himself also showed a decreasing ratio in the later stages of many species, and he suggested Dyar's "constants" should be considered "averages." Thus the situation in *C. alticolella* appears to be typical of the Lepidoptera. This species also conforms with the situation in many other Lepidoptera (see Forbes, 1934) as it has a "Dyar's ratio" greater than 1·26. This value, originally arrived at by Przibram and Megusar (1912), is the expected ratio if the species conforms to the theoretically typical condition of doubling in volume at each moult. They suggested that progression factors greater than 1·26 are due to non-manifested cell-divisions, and Bodenheimer (1933) referred to the latter as "latent divisions" and found them to occur in Orthoptera, Odonata, Rhynchota and especially in the Holometabola.

From the above it is apparent that no instar exists between the four demonstrated. There remain the possibilities that a larval stadium may have been missed at either or both ends of the series already shown to occur. Both these possibilities have been eliminated. Measurements of seventeen first-instar larvae within the egg gave a mean head-capsule width of 1·888 units which differed from the mean for the deduced first-instar (fig. 1) by only 0·087 units, a close agreement. It was also shown that no fifth-stage occurred by measuring cast larval head-capsules found in larval cases after pupation. Measurements of eighteen such head-capsules were within the range of values given in fig. 1 for the width of the head-capsules of fourth-instar larvae.

Fig. 1 might suggest that the width of the head-capsule was more variable in each succeeding instar, but this, however, was at least mainly due to the fact that the same unit of measurement was used for larvae of all four size-groups.

The duration of each larval instar varied considerably, and as many as three different instars were found in some populations at any one time. Such overlap can partly be explained by the protracted oviposition period of about a month. It was also often noted that late, well-fed third-instar larvae were to be found in rush capsules which, if they had remained uninfested, would probably have produced copious ripe seeds. Other capsules,

on the same plant, containing shrivelled seeds, which would probably not have ripened, had within them small, apparently badly nourished, second-instar larvae. As would be expected the food supply available to individual larvae produced marked differences in developmental speeds. In favourable circumstances the first three larval stages were passed through in less than six weeks. Fourth-instar larvae were first observed in 1953, on 8th August, but others did not undergo the final moult until October. Development was much slower in the bad summer of 1954, when the first fourth-instar larva was found on 14th September. Corresponding with the overlap of larval stages there was a marked "succession" in the appearance of larval cases on infested rush capsules. The variable time of appearance of *C. alticolella* larvae is apparently typical of Coleophoridae as a whole (Waters, 1927).

Larvae of *C. alticolella* generally excavated a gallery lined with silk within the rush capsules before constructing the cases which appeared on the exterior of the capsules. In many instances the larvae were enclosed within a complete case of silk within the rush capsules. These cases, like the external ones which were manufactured later, were composed mainly of silk which had seed debris adhering to it. Wood (1892) suggested that the larvae began manufacture of their cases either just before or just after the last moult, following no hard and fast rule. Later, in the same publication, he amended this statement and stated that the operation was begun "shortly after the final moult has taken place." The present investigation has shown Wood's earlier statement to be correct, as a number of third-instar larvae were found with completed larval cases. The silk galleries within the rush capsules were usually begun in this instar, whereas the external larval cases were generally, although not invariably, manufactured by the fourth-instar larvae.

After formation of their cases larvae were free to leave the original rush capsules, and many cased larvae, moved and fed on fresh capsules (see pages 12-13). Larvae completed feeding in the autumn and overwintered as final instar larvae within their cases. This generally took place in the plant litter at the base of the stem, although occasional instances of larvae over-wintering on the rush heads were observed. In the litter the open end of the case was sealed with a barrier of silk, which was sometimes broken before pupation as larvae were observed in movement during mild spells in the winter and also in the spring. The larvae of *C. alticolella* appeared to undergo a true diapause as moths failed to emerge at an early date if larvae were brought indoors to warmer conditions.

Normally larvae of this species did not feed again in the spring, but larvae of *C. glaucicolella* Wood, a closely related species which feeds especially on *Juncus inflexus*, have been observed doing so (Sich, 1923). In the spring of 1953, however, a number of large larvae of *C. alticolella* were found feeding on the developing rush capsules of the new year's growth. This occurred after some adult moths had emerged and, in some cases, after the last adult was recorded in the area. There is evidence which suggests that one possible reason for this occurrence was a lack of food, in the form of rush capsules containing ripe seeds, in the autumn of 1952. Waters (1927) suggested another explanation for the same phenomenon observed with two larvae of

C. solitariella Zell. which he collected in mid-July and which is normally adult by June. One of these larvae remained alive until the following spring and then produced an Ichneumon, and he suggested that *Coleophora* larvae which failed to pupate at the usual time were all parasitised. However, late feeding larvae in the Moor House area were generally found not to be parasitised, although a few proved, on dissection, to contain a larva of Ichneumon type. As is shown on page 9 these were not a common parasite of *C. alticolella*, at least in this area, as the apparently most important Ichneumon parasite had an externally feeding larva and, in fact, destroyed its host before the onset of winter.

(c) *Pupa*

Pupation of overwintered larvae began about mid-May but living larvae were found as late as 18th June, and it is known that pupae occurred as late as the end of August as some moths did not emerge until this date in the laboratory. The shortest pupal period observed was three weeks.

Before pupation, the larvae turned around inside their cases, and the imagines emerged through the apical valves. As the pupae were orientated with their anterior ends at the apex of the cases it seemed most likely that the larvae reversed their original orientation during the process of pupation—certainly larvae found just prior to pupation had their heads still at the original end of the larval cases.

(d) *Imago*

Observations made in 1953 and 1954 suggested that a warm dry spell stimulated emergence. In both seasons the main emergence of *C. alticolella* began in early June, although occasional early specimens were recorded. For instance, in 1954, one specimen was taken on 31st May and then no more were recorded until many appeared on 8th June. Field observations suggested that there was little, if any, difference between the dates of first emergence at various heights. These observations agreed with those of Pearsall (1950).

Dissection of newly emerged female moths showed that ten to twenty eggs were apparently of full size and ready for immediate laying. In addition to these eggs there were large numbers of eggs decreasing in size towards the distal ends of the ovarioles. Mr. R. C. Reay (personal communication) recorded a total of 124 eggs laid by a single female in captivity before the moth died after eighteen days. It seems that the majority of these eggs can be matured and deposited in the course of the insect's life, as females towards the end of each season, were generally found to contain only a few large eggs; one was found to contain only a single egg. Fertilisation occurred very soon after emergence and most females collected a day after the main emergence in the field were found to have a swollen bursa copulatrix, with one or more spermatophores present. As many as five were recorded in a single individual.

C. alticolella was recorded ovipositing on both *J. squarrosus* and *J. effusus*. Close examination did not reveal any apparent difference between the

individuals visiting the two rushes, and the paler "effusus" variety referred to by Wood (1892) and Waters (1928) was not found in the area. There were no obvious colour differences in the series of adults collected in the study area, and the few recorded instances of oviposition on *J. effusus* were probably chance visits by the darker "squarrosus" form. This is the typical moorland form of the species, the paler form having been recorded mainly in lowland woods and damp places where *J. effusus* occurs, but not *J. squarrosus*.

In 1953 the last adult was observed in the field on 3rd July, but in the following year adults were present until 17th July. In the laboratory emergence occurred as late as 24th July and one individual remained alive until 2nd August.

Eleven newly emerged specimens kept in the laboratory in 1953 had a mean longevity of 20·8, S.D. $\pm$ 6·11 days. These were given and observed to take, sucrose solution. Altogether many more individuals collected from field sources were kept in the laboratory throughout the emergence period. The last of these individuals, which was provided with sucrose solution, died on 5th July, which compares closely with the date (3rd July) on which living adults were last observed in the field. One individual lived in captivity for thirty-five days.

During 1954 larger numbers of adult *C. alticolella*, kept in the laboratory over the period of adult activity, were placed four per honey-jar and were provided with filter paper which, in an equal number of instances, was kept dry, kept damp with tap water or kept damp with a saturated sucrose solution. Moths were found to take up both free water and sucrose solution in the laboratory. Three further jars were set up with three moths in each to act as replacements if any of the other moths either died prematurely by becoming stuck to the filter paper or escaped when the filter paper was being recharged. The moths were all collected on the three days 8th-10th June at a locality which had been kept under prior observation. It was estimated that few, if any, of the individuals used in the experiment were more than three days old when collected. Each day's collection of moths was divided equally between the three treatments.

Thirty-nine moths kept in dry conditions lived for 7·00, S.D. $\pm$ 3·06 days; thirty-five individuals provided with water lived for 17·43, S.D. $\pm$ 6·28 days; thirty-nine provided with sucrose solution, for 19·00, S.D. $\pm$ 4·62 days. The difference in longevity between those moths kept under dry conditions and the remainder was obviously considerable but an analysis of variance (table 1) has been carried out to determine whether the difference in longevity between those moths which were provided with water and those provided with sucrose solution, was an effect of the two treatments or due to individual variation between the moths.

The value for F is above the 5% level and near the 1% level. This suggests that feeding on sucrose solution probably increased longevity, but by only a slight amount. The maximum longevity in captivity in 1954 was thirty-four days (thirty-five days in 1953), and this individual was provided with water only. Feeding by adult *C. alticolella* was never observed in the field (see

page 2) and these laboratory experiments show that it is not necessary to postulate feeding by the imagines under natural conditions. However, a source of free water does appear necessary for existence over about a week, and even in the driest years, this is provided by early morning dew. Imagines were observed to take in this liquid in the field.

TABLE I

Analysis of variance of the longevity of moths which were provided with water or sucrose solution

Source of variation	Sums of squares	Degrees of freedom	Variance estimate
Between treatments	60·89	1	60·89
Within treatments	718·73	72	9·98
Total	779·62	73	

$$F = \frac{60 \cdot 89}{9 \cdot 98} = 6 \cdot 10$$

It seems that even a short period of dry weather might quickly reduce a population of *C. alticolella* nearing the end of its life-span. In the study area such a period of weather occurred in 1953, at the time of a sudden disappearance of the moths. During the period of adult activity in 1954 the weather was consistently wet, no sudden disappearance was noted, and the date of ultimate disappearance was a fortnight later than in the preceding year.

(e) *Parasites*

In some areas large numbers of larval cases of *C. alticolella* were observed on rush capsules throughout the winters of 1952-53 and 1953-4. Although some of these contained healthy larvae or larvae which had died from unknown causes, the majority were found to contain larvae attacked by parasitic Hymenoptera. Parasitised larvae were only rarely found in the plant litter and these were mainly individuals attacked by an internal parasite, referred to on page 9, which did not destroy its host until the spring and caused failure to pupate. The major parasites in the area were found to have externally feeding larvae and to kill their hosts before they were ready to migrate from the rush capsules to the litter. The four species of parasite identified from the study area were all induced to emerge at an early date indoors, some by the beginning of December after only three weeks in the laboratory.

The four species of Hymenoptera bred from *C. alticolella* larvae have been identified as *Ephialtes* (*Scambus*) *brevicornis* Grav. (Ichneumonidae), *Bracon* sp. (Braconidae), a species of a genus near *Miotropis* (Eulophidae) and an unidentified species of Pteromalidae (males only obtained). These are all apparently new parasite records for the species. Thompson (1945) recorded four other Hymenoptera, *Gelis instabilis* Forst. (Ichneumonidae), *Hemiteles* sp. (Ichneumonidae) *Microbracon obscurator* Nees. (Braconidae) and *Microbracon osculator* Nees (Braconidae).

In the present investigation only *Ephialtes brevicornis* and the Eulophid (referred to hereafter as "*Miotropis*") were recorded in large numbers. Only one specimen of the Braconid and twelve male Pteromalids occurred in the total of over 200 parasite specimens which were bred in the laboratory.

No parasites were observed attacking *Coleophora* larvae in the field and the manner in which they reached the larva inside its case is unknown. Sich (1923) suggested that the larger species of parasite could pierce the larval case with their ovipositors whereas the smaller Chalcid parasites entered the case through the apical valves.

In the laboratory many male *Ephialtes brevicornis* emerged before the appearance of the first female and, although females were in larger numbers amongst the later emerged individuals, males still predominated. Adult *E. brevicornis* were collected from the field between early May and late August in both 1953 and 1954. The adult insect left the larval case by a characteristic round hole which it bored in the case wall. In both years these emergence holes were observed about a month before the moths began to emerge (it has already been shown that *Ephialtes* rapidly emerged once brought into the warmer conditions of the laboratory). No information is available about other possible host species in the study area. According to to Mr. J. F. Perkins (personal communication) the many hosts of this species are usually species that live in flower heads or compact buds.

During early August, 1953, much activity was observed by female *Ephialtes* flying amongst the rush heads, on which the first *Colephora* larval cases were just appearing, and it is suggested that oviposition occurred about that time. The females were very active and flew off after even the slightest disturbance. Young *Ephialtes* larvae occasionally numbered more than one per host, but no instance of more than one full grown larva in a rush capsule was observed. Attacked larvae were killed before mid-September and *Ephialtes* over-wintered as larvae in the rush capsules or in the empty *Coleophora* cases attached to the capsules.

Adult "*Miotropis*" were not observed in the field. Attacked *Coleophora* larvae were destroyed in the autumn and the parasite overwintered as pupae, of which up to three were observed per host, in the same situations as *Ephialtes*. Morley and Rait Smith (1933), referring to the genus *Coleophora*, suggested that some of the Chalcid parasites may be hyperparasites. This was not so with "*Miotropis*" which attacked Coleophora directly.

3. Behaviour

(a) *Final instar larva*

After the time spent feeding within the original rush capsule, a *Coleophora* larva may sever the connection of the larval case to the capsule and move off, bearing the case. In a few instances larvae moved immediately to the litter, and remained there during the winter but the majority of the larvae reached other rush capsules, bored into them, and began to feed on the contained seeds. In some areas practically all capsules of *J. squarrosus* had been attacked by the end of the summer. Such capsules, after the larva

responsible for the damage had left, contained a mass of seed debris with only a few intact seeds remaining. During the larval wanderings any upright stem or blade of grass was climbed and it was through this reaction that atypical food plants (such as *Luzala campestris*, referred to on page 2) were reached.

Silk threads assisted in larval movement and larvae in their cases were often seen suspended by them from the apices of rush stems. When blown by the wind, the threads often became entangled around a neighbouring stem and the larvae were thus assisted in becoming established on a new rush plant. Larvae were occasionally observed to move from a rush capsule into its immediate neighbour by boring through the wall of the first rush capsule and into that of the second. In such instances the larval case remained attached to the original capsule.

In 1953 field experiments were carried out on the movement of the final instar larvae. Larval cases and the rush capsule on which each case originally appeared were marked in a similar way with spots of coloured lacquer. Capsules subsequently fed on by a marked larva were marked in an identical manner. A total of 295 larvae were marked in two experimental areas. One area (site A) was at 1,525 ft. on the eastern slopes of the Pennines and here 101 larval cases were marked on the day of their first appearance on the rush capsules in early August. The other area (site B) was at Moor House (1,840 ft.) where eight sods of *J. squarrosus*, from site A, were planted out at the beginning of August, and 194 larvae which appeared on these plants were marked on the day of their appearance during the succeeding weeks.

At site A, for the first fortnight after marking, observations of larval movement were made daily but, after this time, it became apparent that a larva only rarely moved on consecutive days and the time between observations was increased to three days. Regular observations were discontinued on 8th September, by which time eighty of the original 101 larvae had disappeared. A final observation was made on 26th September, when only five of the original larvae remained; four of these were dead, and had not moved since they were originally marked, and the fifth was attached to the stem of a rush plant and would presumably have overwintered there. During the period of the marking experiment four of the original sixty-seven stems on which larvae were marked were eaten by sheep, with the consequent loss of some larvae. These larvae are omitted from further discussion.

For the purpose of the calculations which follow it has been assumed that all the larvae which disappeared from the rush capsules in the course of the experiment had passed into the litter prior to overwintering. This seemed to be a valid assumption, because all rush stems in the vicinity were closely examined for some days before any larvae were recorded as having completed their feeding. Further evidence to support this assumption was gained from the plants in the experimental plot at Moor House (site B). There larvae began to disappear at approximately the same date, and in comparable numbers to those at site A, and at site B the larvae could not have moved to a new rush stem, and escaped observation, as all the rush plants in the plot were artificially transported there, and all were kept under observation.

Despite the fact that all the marked larvae alive in mid-September had completed their feeding there were still considerable numbers of unmarked larvae on the rushes in the area at that time. These larvae were those whose external larval cases were manufactured after the external cases of the marked larvae appeared. This "succession" of stages in the life history of the insect has already been referred to and reasons for its occurrence suggested (page 6).

The technique outlined above enabled the number of capsules attacked by individual larvae to be determined. In the following calculations only those larvae (eighty of the original 101 which were marked) which had completed their feeding by 8th September are considered. Up to this date observations were sufficiently regular to record all the capsules which were attacked by

TABLE II

Capsules of *J. squarrosus* attacked by marked larvae of *C. alticolella* in 1953

(i) Site A

Number of capsules fed on	Number of larvae
1	15
2	35
3	20
4	6
5	2
6	2

Totals: Capsules 191, larvae 80
Mean consumption per larva = 2·39 capsules

(ii) Site B

Number of capsules fed on	Number of larvae
1	18
2	48
3	20
4	6
5	1

Totals: Capsules 203, larvae 93.
Mean consumption per larva = 2·18 capsules

the marked larvae. It should be noted that there was a variable amount of destruction of seeds in the capsules which were attacked, but, by the end of the summer, in regions of heavy infestation (as in this area in 1953), very few mature capsules remained unattacked and only occasionally were a few viable seeds present in capsules which had been attacked by the larvae. The destruction caused in a particular capsule was, in a few limited instances, due to more than one larva. The error this factor introduces is small because

most larvae destroy two or more capsules and it was a general rule that when a larva was attached to one capsule for at least four to five days (and this was usually the case, as will be shown later) it consumed at least the major part of the contents itself. The seeds in the capsule within which the early part of larval development took place were usually all consumed, but the degree of destruction in the subsequent capsules which were visited varied.

The eighty larvae in question visited a total of 191 capsules before their feeding was completed. Table II (i) shows the number of capsules visited by each of these larvae.

At site B 194 larvae were marked over the period 11th August-7th September. By 8th September, when regular observations were discontinued, ninety-three of these had finished feeding and the following calculations are limited to these larvae. These ninety-three larvae visited a total of 203 capsules, and Table II (ii) shows the number of capsules visited by each larvae.

From Table II it can be seen that there was a close similarity between the mean number of capsules consumed per larva at site A (2·39) and site B (2·18).

The eighty larvae from site A together with thirty-seven of the larvae from site B, which were marked at the same time, were divided up into groups according to the number of rush capsules they attacked during their life.

TABLE III

The number of days spent on rush capsules by various groups of *C. alticolella* larvae

Number of capsules fed on	Number of larvae	Mean number of days spent on rush capsules	Mean number of days spent per capsule
1	20	17·5±8·5*	17·5
2	54	18·2±7·3	9·1
3	32	20·8±5·7	6·9
4	7	19·7±5·0	4·9
5	2	26·0	5·2
6	2	19·0±6·0	3·2

*Standard deviation.

Table III shows that the average number of days spent feeding on the rush stems did not vary appreciably despite the absolute number of capsules attacked. Thus the average time spent on each individual capsule tended to decrease as the total number of capsules attacked increased. This suggests that a fairly uniform period of just under three weeks was required for feeding after the formation of the larval case, and that some larvae, which remained on their original rush capsule, probably consumed considerably fewer fresh seeds than other more mobile larvae in the same length of time.

During their feeding period larvae were not limited to capsules on their original stem and, of the 173 larvae on which the results given in Table II

were based, 35 (20·2%) had moved to one new stem, four (2·3%) to two new stems and one (0·6%) to three new stems before finishing feeding and moving off into the litter. In some instances adjacent rush inflorescences were in contact and thus a journey through the basal vegetation mat was not involved. In other instances, however, this was not so and one larva, for example, moved more than two feet through the vegetation mat in the course of four days, from one stem to another. Movement was random and larvae were observed moving down one stem and then turning round and beginning to feed again on a new capsule on the same stem.

There did not appear to be any periodicity in larval movement. Larvae were observed in movement during all the daylight hours and some larvae, whose positions were recorded just before nightfall, were noted feeding on new capsules early on the following morning.

Hand-sorting of vegetation litter in the laboratory showed that *C. alticolella* larvae overwintered in the loose upper layers of the litter. Here they would be subjected to considerable temperature fluctuations as well as to the danger of becoming waterlogged. A simple laboratory experiment was devised to determine whether *Coleophora* larvae could survive in the upper layers of the plant litter in temperatures below freezing point. Ten marked *Coleophora* larval cases, each containing a living larva, were placed on a clump of *J. squarrosus* which, two days later, was placed in a refrigerator and crushed ice put on the litter surface. The temperature of the litter surface was maintained at −2°C. to −4°C. A fortnight later the litter was hand-sorted, and all ten marked larvae were recovered alive from the surface layer. One larva was recovered with its case firmly affixed to a piece of ice. By remaining in the surface layers of the litter at the base of the rush plants the larvae were not so exposed to the danger of becoming waterlogged as they would have been if they had buried themselves deeper. Even so the risk of drowning must have been considerable, as, during the heavy winter rains, some areas were under water for several days.

Sich (1923) stated that the larval case is lined with a substance impervious to water and, during the present investigation, it was found that the case is difficult to wet externally.

(b) *Imago*

Under natural conditions the moths were relatively inactive and they were only rarely found flying more than one to two feet above the vegetation. They were observed to spend much of their time on the developing rush stems and surrounding vegetation, with brief flights of rarely more than six feet. Flying activity was reduced in windy conditions when the moths sheltered quite deep in the vegetation mat. Flying was also observed at night.

Pairing was observed both in the field and the laboratory. Pairs were generally found stationary on upright vegetation in end to end posture. In the laboratory pairing lasted up to nine hours. Mating was at its peak among newly emerged moths, but isolated pairs were observed throughout the period of adult activity.

Oviposition was observed during both day and night and continued throughout the period of adult activity.

Except for dew-imbibing no feeding by adult *C. alticolella* was observed in the field. The only plants in flower at the time of adult activity were *Potentilla erecta* (L) Räusch and *Galium hercynicum* Weigel but no visits to these flowers were observed in the field or when moths were confined in jars with fresh flowers. In the laboratory, but not in the field, adult *Coleophora* were observed feeding on Cercopid "cuckoo-spit" and this, an extremely abundant substance at the time of the adult emergence, was a possible food-source in the field. These field observations, and the laboratory experiments described on pages 8-9, suggest that *C. alticolella* does not normally feed in the adult stage, except for water intake.

4. Summary

1. In 1953 and 1954 adult *C. alticolella* were to be found on moorland in the northern Pennines from early June to mid-July. Oviposition occurred throughout this time and eggs were laid under the perianth segments of *J. squarrosus* flowers and between adjacent flowers.

2. The larvae fed on the seed capsules of *J. effusus*, *J. articulatus* and *Luzula campestris*, in addition to *J. squarrosus*, the main food plant in the area.

3. Four larval instars occurred and third- or fourth-instar larvae manufactured a silken case and became potentially mobile. Feeding was completed in the autumn and overwintering of cased larvae normally occurred in the upper layers of the litter at the bases of rush plants. Pupation occurred in the spring.

4. Dissection of female moths showed that there were at least ninety eggs present on emergence. Ten to twenty of these appeared ready for immediate oviposition.

5. The mean longevity of moths kept in the laboratory and given no liquid was 7·00 days, for those given water 17·43 days, and those given sucrose solution 19·90 days.

6. Four species of parasitic Hymenoptera were reared from larvae, the two commonest being *Ephialtes* (*Scambus*) *brevicornis* (Grav.) (Ichneumonidae) and a species of a genus near *Miotropis* (Eulophidae).

7. Marking experiments showed that final-instar larvae visited a mean of 2·39 rush capsules in one area, and 2·18 capsules in another, during their feeding period. After formation of the case a mean period of about three weeks was spent on rush stems irrespective of the number of capsules attacked by each larva.

8. The imagines were found to be relatively inactive. Pairing and oviposition in the field and the laboratory occurred both during the day and night. The moths were not observed to feed in the field and it is suggested that a supply of free water is sufficient for survival under natural conditions.

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